

INTRODUCED AND NATIVE POPULATIONS OF A MARINE PARASITIC CASTRATOR: VARIATION IN PREVALENCE OF THE RHIZOCEPHALAN *LOXOTHYLACUS PANOPAEI* IN XANTHID CRABS

Anson H. Hines, Fernando Alvarez and Sherry A. Reed

ABSTRACT

Patterns of prevalence and host specificity of the parasitic castrator, *Loxothylacus panopaei*, in a region of parasite introduction (Chesapeake Bay, Maryland-Virginia) were compared to those within its native geographic range (Indian River Lagoon, Florida). Prevalence in five species of xanthid crabs was measured at several spatial and temporal scales along the east coast of North America. The parasite infected *Panopeus lacustris*, *P. simpsoni*, *P. obessus*, *Eurypanopeus depressus*, *Dispanopeus sayi* (reported as a host for the first time), and *Rhithropanopeus harrisi*, but did not infect *P. herbstii*. The overall prevalence of infection in over 10,000 crabs was low (< 1%); but prevalence exhibited significant large scale geographic variation from 0-83% in the parasite's disjunct distribution along 2750 km of coast and 14 degrees of latitude from New Jersey to western Florida. The introduced range of the parasite included most of Chesapeake Bay, outer Delmarva Peninsula, and North Carolina sounds; but the parasite was not found from South Carolina to Cape Canaveral, Florida. The native range extended from the Gulf of Mexico and eastern Florida up through the Indian River Lagoon. Significant temporal variability of infections occurred between 2 yrs along the geographic range of sampling, with the parasite occurring sporadically (0-47%) in introduced regions of North Carolina and (0-83%) in coastal Virginia. The prevalence of parasitism also exhibited significant local variation among sites within the introduced region of Chesapeake Bay (0-91%) and the native region of the Indian River Lagoon, Florida (0-9%). Parasite prevalence within the Indian River Lagoon exhibited long-term (12 yrs) relative temporal stability at about 7.5% in *P. lacustris*. In contrast, the parasite exhibited epidemic out breaks (0-72%) in a 15-yr record at the Rhode River subestuary of Chesapeake Bay following its slow spread over 200 km in 30 yrs from introduction in the lower bay in 1963. Size of infected hosts was relatively constant for each crab species, resulting in all sizes of *R. harrisi* and *E. depressus* being infected but larger *P. lacustris* not being infected. Despite the parasite's impact on crab reproduction, the host-parasite interaction is apparently stabilized by shifting combinations of four factors: host species composition; recruitment dynamics, especially slow parasite dispersal; patchy host dispersion in oyster reefs; and reservoirs of uninfected hosts resulting from refuges in host size (e.g., large *P. lacustris*) or host habitat distribution (e.g., low salinity for *R. harrisi*).

Ecological and evolutionary models of host-parasite population dynamics are often based on assumptions about spatial and temporal variation of infections as factors which determine the stability of the parasite-host interaction and allow the persistence of a deleterious parasite within a host population (May and Anderson, 1979; Anderson and May, 1979; Hassell and May, 1989). Despite their theoretical importance, the interaction of spatial and temporal variables is rarely measured for natural populations of marine parasites (Lauckner, 1983; Craig et al., 1989; Lively, 1989; Crosby and Roberts, 1990). Host species diversity and infection demographics are key attributes of host specificity that define the dynamics of parasite resource utilization (Caswell, 1978; Hood and Welch,

1980; Bush and Holmes, 1986a,b; Stock and Holmes, 1987). Parasites are typically characterized as generalized or specialized, and host life stages are assessed for vulnerability to infection (Esch et al., 1990). However, host specificity in marine parasites is not well studied (Goggin et al., 1989).

Population dynamics of many parasitic species are characterized by epidemics, and epidemics in terrestrial systems often result from introductions of exotic pathogens into new geographic regions and hosts (Elton, 1958; Bailey, 1975). Although introductions of invertebrate species have been common in estuarine and protected coastal ecosystems for 300 yrs (Carlton, 1987; 1989; 1992; Carlton and Geller, 1993), introductions of parasites in these habitats have been documented only rarely. For example, the apparent introduction of the haplosporidian *Minchinia nelsoni* into Delaware Bay in 1959 spread rapidly to Chesapeake Bay, producing epidemic infections and mortality of oysters (Andrews, 1979). Epidemics and rapid spread of disease in some marine ecosystems (Lessios et al., 1984) could be attributed speculatively to introductions of parasites to new regions and/or to new host species. However, the histories of introductions for parasitic and non-parasitic species alike are often poorly understood in marine ecosystems (Carlton, 1996).

Population dynamics of parasitic castrators provide insight into the ecological stability of host-parasite interactions and the evolution of reduced virulence (Kuris, 1974; Obrebski, 1975; Levin and Pimentel, 1981). Parasitic castrators act in a manner similar to entomophagous parasitoids, in that they are relatively large compared to the host and they eliminate the host's reproductive contribution (Kuris, 1974). Although parasitic castrators do not kill their hosts as do parasitoids, they may be important regulators of host population density (Kuris, 1974). Marine parasitic castrators may have significant impacts on ecologically and commercially important hosts (Blower and Roughgarden, 1987a,b; 1988; 1989; Kuris and Lafferty, 1992). Imposing reproductive mortality upon the host, these parasites may be viewed as evolving minimal virulence by attacking primarily gonadal tissues while leaving the host otherwise apparently unharmed (Obrebski, 1975). Thus, at the level of the individual host, the parasite has evolved a stable interaction; whereas paradoxically at the level of the population, the host-parasite relationship may be highly unstable. The scale of spatial patchiness and temporal variability of parasite prevalence, as well as host specificity, are important variables which reflect parasite dispersal and host vulnerability, and which affect stability of the host-parasite interaction at the population level (Reeve, 1990; Hassell and May, 1989; Comins et al., 1992; Kuris and Lafferty, 1992). However, these interactions are poorly understood in marine parasitic castrators.

Rhizocephalan cirripedes are important parasitic castrators of anomuran and brachyuran crabs in marine ecosystems. Many species are considered to be host specialists, while others have broad geographic distributions and infect several related host species (Boschma, 1955; Reinhard, 1956). However, analyses of spatial variation in rhizocephalan infections across large geographic distances are unusual (Heath, 1971; O'Brien, 1984; Weng, 1987; Hochberg et al., 1992), and characteristics of their long-term temporal variation are not known.

Here, we compare populations of the rhizocephalan *Loxothylacus panopaei* infecting several species of xanthid crabs within its native and introduced ranges of distribution along the east coast of North America. The reported native distribution of *L. panopaei* extends through the Gulf of Mexico infecting *Panopeus herbstii*, *Eurypanopeus depressus*, and *Tetraxanthus rathbunae*, and into the Caribbean to Venezuela infecting *Tetraplax*

quadridentata and *Panopeus occidentalis* (Boschma, 1955). The parasite was also introduced inadvertently into Chesapeake Bay in 1963, apparently with infected *E. depressus* associated with oysters transplanted from the Gulf of Mexico into the York River (Van Engel et al., 1966). Although *L. panopaei* established successfully and spread from the site of introduction into the lower Chesapeake Bay (Daugherty, 1969), its distribution and host-parasite interactions in the region have not been studied, except for certain features of the parasite's biology (Reisser and Forward, 1991; Walker et al., 1992; Grosholz and Ruiz, 1995; Alvarez et al., 1995). The life cycle of this parasite includes a planktonic nauplius and infective cypris, which converts to a kentrogon upon attachment to the crab host (Walker et al., 1992). The kentrogon injects primordial cells into the host, and an internal parasite grows to castrate the host and to produce an external brood sac (the *sacculina externa* or, simply, the *externa*) under the crab's abdominal flap, completing the life cycle in about 1 mo (Høeg, 1991; Walker et al., 1992; Alvarez et al., 1995).

Our sampling design allows us to consider the interaction of spatial and temporal variability in parasite prevalence at several scales. We measured spatial variation in parasite prevalence at two scales: geographic variation along 2750 km of coastline from New Jersey to Florida; and local variation within the Indian River Lagoon and Chesapeake Bay representing regions within the native and recently introduced geographic ranges of the parasite, respectively. Our purposes were: to determine the parasite's geographic distribution along the east coast of North America, assessing both the limit of the parasite's native range and the extent of the parasite's spread; to estimate the scale of patchiness in parasite prevalence within regions of native and introduced parasite populations; and to determine the species diversity of hosts infected by the parasite in regions of established and introduced parasite populations. Similarly, we assessed temporal variability in the parasite's prevalence at two levels: annual variation was measured between 2 yrs along the geographic range of sampling; and long-term (12-15 yrs) variation was measured for two local sites within the regions representing the native and the introduced populations. Our purposes were: to assess the stability of parasite prevalence over a broad geographic area; and to compare dynamics of parasite prevalence in host populations within established and introduced regions of the parasite. We also analyzed the population size structure of infected and uninfected crabs of three host species to determine minimum and maximum sizes of parasitized individuals, which allowed us to assess if host populations included sizes ranges of mature crabs that were invulnerable to infection.

METHODS

Populations of xanthid crabs were sampled at locations along the east coast of North America from New Jersey to Florida extending into the eastern Gulf of Mexico and within two widely separated regions in Chesapeake Bay, Virginia-Maryland and the Indian River Lagoon, Florida (Fig. 1). Four types of sampling schedules were employed to determine spatio-temporal patterns of variation in parasitism. (1) To determine annual and large-scale geographic variation spanning the reported native and introduced ranges of *L. panopaei*, crabs were sampled at single sites for 18 locations along the Atlantic coast (Fig. 1) during low tides in discrete 2-yr periods in June-August 1983 and again in April-June 1986. (2) To provide further resolution of the large-scale geographic distribution of the parasite within its native and introduced ranges, crabs were sampled later at supplementary sites (Neuse River, North Carolina and 8 sites along the west coast of Florida) (Fig. 1) during 1993; (3) To determine regional-scale geographic variation within the established and the introduced ranges of the parasite, crabs were sampled during a single time during June-August

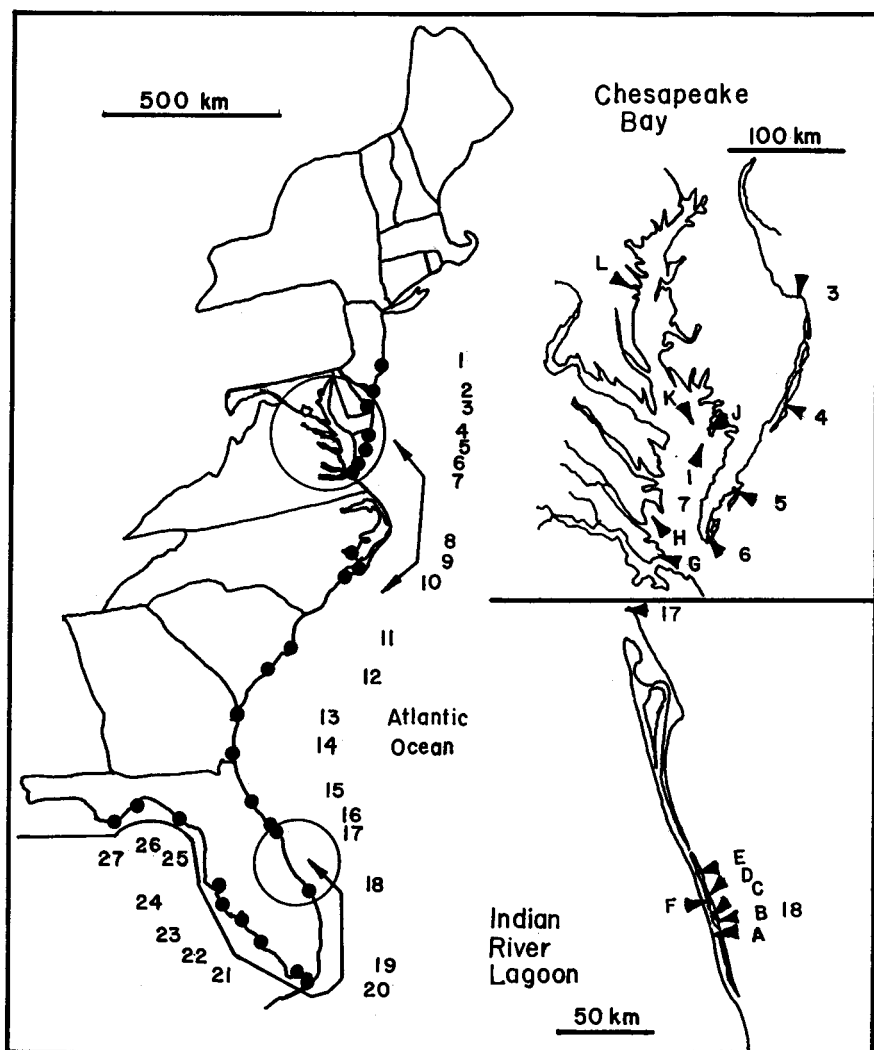


Figure 1. Collecting sites of xanthid crabs for determining prevalence of *Loxothylacus panopaei* along 2750 km of the east coast of North America from New Jersey to Florida. Circles indicate location of insets for Indian River Lagoon, Florida, and for Chesapeake Bay, Maryland-Virginia. Numbers 1-7, 9-19 indicate sites listed in Table 1; sites 8, 20-27 in Table 2; sites A-F in Table 3; sites G-L in Table 4. Lines with arrows indicate parasite presence, showing disjunct distribution of parasite introduction in Chesapeake Bay, as well as part of native range in Florida.

1983 from six sites within the Indian River Lagoon, Florida and from six sites within Chesapeake Bay, Virginia/Maryland (Fig. 1). (4) To determine long-term variation in parasite prevalence at locations of the regions within the established and the introduced geographic ranges of the parasite, crabs at individual sites were sampled many times over a period of 12 yrs from 1982 to 1993 in the Indian River Lagoon and 15 yrs from 1979 to 1993 in the Chesapeake Bay.

Crabs were sampled with field collections that were preserved and later processed in the laboratory. For most samples, crabs were collected haphazardly by hand during low tides in the intertidal zone from similar habitats on muddy sand under rocks and cobble, along breakwaters, or in oyster bars in high salinity (>25‰), sheltered bays. However, in Chesapeake Bay crabs were collected

subtidally from oyster shell <10 m deep by dredge or from submerged logs <1 m deep by hand; and samples at three sites (St. Lucie River, Florida; Neuse River, North Carolina; and Rhode River, Maryland) were taken at low salinities of 8-15‰. All of the xanthid crabs found at each site were collected to avoid biasing the sample by crab size or species. Sample sizes for each collection ranged from 11 to 674 crabs per species, with most (64%) collections consisting of >50 crabs and often (36%) >100 crabs. The collections were fixed in 10% formaldehyde seawater for 7 d before transfer to 70% EtOH for storage. Stored samples were later sorted, identified to species, and each crab examined for the presence of *sacculina externae* (hereafter called *externae*) or brooded eggs under the abdomen. Maximum carapace width of parasitized and non-parasitized crabs were measured in samples with individuals bearing an *externa*.

Prevalences of parasitic infection in host samples were calculated as the number of individuals of a host species infected with the parasite divided by the number of hosts examined, and expressed as a percentage (Margolis et al., 1982). Statistical treatments included: log-linear models for categorical data testing effects of host species, year, sampling site, and their interactions upon prevalence of parasitism; and ANOVA for comparisons of log-transformed carapace widths of parasitized crabs among years (Sokal and Rohlf, 1981).

RESULTS

GEOGRAPHIC VARIATION ALONG EASTERN NORTH AMERICA. —During 1983 and 1986, a total of 6128 xanthid crabs was sampled from intertidal, high salinity habitats at 18 locations along the approximately 2000 km transect over 14 degrees of latitude from Egg Harbor, New Jersey to Flamingo, Florida (Fig. 1). In 1983, 3450 of these crabs were collected in June-August from 12 sites; in 1986, 2678 crabs were collected in April-August during revisits to six of these sites plus six additional sites. Four species of Xanthidae comprised the collections: 55% *Panopeus herbstii*; 7% *Panopeus lacustris*; 23% *Eurypanopeus depressus*; and 15% *Dispanopeus sayi* (Table 1).

Crabs with *externae* were rare in these collections of the four potential host species: a total of only 83 crabs (1%) were infected, but prevalences of *L. panopaei* ranged from 0-83% in samples of these species. Considering the 1983 and 1986 collections combined, log-linear models revealed that prevalences varied significantly among host species ($X^2 = 63.97$, $df = 3$, $P < 0.001$) but not among locations ($X^2 = 12.33$, $df = 17$, $P > 0.9$), or between years ($X^2 = 0.16$, $df = 1$, $P > 0.6$); however there were significant Host*Site ($X^2 = 76.49$, $df = 51$, $P < 0.02$) and Site*Year ($X^2 = 43.84$, $P < 0.001$) interactions. No *P. herbstii* in these collections was infected; however, 4.9% of *P. lacustris*, 3.6% of *E. depressus*, and 0.4% of *D. sayi* had *externae* of *L. panopaei*. Infected crabs were found only at five locations: Chincoteague and Quinby, Virginia, in *E. depressus*; Chesapeake Bay in *E. depressus* and *D. sayi*; Bogue Sound, North Carolina, in *E. depressus*; and Fort Pierce, Florida, in *P. lacustris* and *E. depressus*. Rhizocephalan parasites were absent from all samples along the coast from South Carolina to northern Florida. Since *P. herbstii* was not infected in any sample, and since there were significant interaction terms, we re-analyzed the data excluding this species for each year separately. In 1983 prevalence differed significantly among the 3 host species ($X^2 = 14.49$, $df = 2$, $P < 0.001$) and not among sites ($X^2 = 8.09$, $df = 8$, $P > 0.4$), but there was a significant Host*Site interaction ($X^2 = 47.08$, $df = 16$, $P < 0.001$). In 1986 prevalence differed significantly among the three host species ($X^2 = 18.77$, $df = 2$, $P < 0.001$) and among sites ($X^2 = 26.44$, $df = 9$, $P < 0.002$), with no significant interaction terms. Considering only the six sites with samples for both years while excluding *P. herbstii*, prevalence differed significantly among host

Table 1. Prevalence of *Loxothylacus panopaei* in xanthid crabs sampled from 18 locations along the east coast of North America in 1983 and 1986. Numbers indicate percent of sample bearing externae (no. of crabs in sample)

Map Loc. Site	Dates	<i>Panopeus herbstii</i>		<i>Panopeus lacustris</i>		<i>Eurypanopeus depressus</i>		<i>Dispanopeus sayi</i>	
		1983	1986	1983	1986	1983	1986	1983	1986
1 Ocean City, NJ	7/22/83	0 (18)				0 (311)		0 (24)	
2 Cape May, NJ	7/21/83	0 (83)				0 (26)			
3 Cape Henlopen, DE	8/9/83	6/22/86	0 (74)						
4 Chincoteague, VA	7/10/83	6/23/86	0 (168)			0 (44)	16.7 (12)		
5 Quinby, VA		6/21/86	0 (283)				83.3 (24)		
6 Kiptopeake, VA	8/9/83	0 (26)						0 (674)	
7 Chesapeake Bay, VA/MD	8/1/83	0 (326)				9.7 (155)		1.6 (250)	
8 Beaufort, NC		4/27/86	0 (148)					0 (24)	
9 Bogue Sound, NC	7/7/83	4/26/86	0 (179)			47.4 (38)		0 (55)	
10 North Inlet, SC		4/25/86	0 (286)					0 (20)	
11 Charleston, SC	6/21/83	4/24/86	0 (341)						
12 Savannah, GA		4/24/86	0 (122)					0 (60)	
13 Jekyll Island, GA	6/20/83	4/23/86	0 (191)			0 (48)		0 (29)	
14 St. Augustine, FL		4/22/86	0 (227)					0 (13)	
15 Edgewater, FL		4/21/86	0 (139)					0 (25)	
16 Port Orange, FL	6/28/83	0 (113)							
17 Fort Pierce, FL	6/17/83	4/20/86				3.3 (153)	7.2 (207)	0.7 (144)	0.5 (389)
18 Flamingo, FL	6/15/83					1 (48)		0 (12)	
Total by host species by year =		0 (1523)	0 (1820)	3.0 (201)	7.2 (207)	4.3 (778)	3.7 (651)	0.4 (948)	
Total by host species for both years =			0 (3343)	4.9 (408)			4.1 (1429)	0.4 (948)	

Table 2. Prevalence of *Loxothylacus panopaei* in xanthid crabs sampled from North Carolina and Florida during 1993. Map Loc. refers to Figure 1. Numbers in table: percent of sample bearing externaenae (no. of crabs in sample)

Map			<i>Panopeus lacustris</i>	<i>Panopeus simpsoni</i>	<i>Panopeus obessus</i>	<i>Eurypanopeus depressus</i>	<i>Rhithropanopeus harrisi</i>
NORTH CAROLINA							
8	Neuse River	8/29/93					22 (324)
FLORIDA							
20	Key Largo	7/22/93	2.4 (41)				
21	Naples	7/18/93		1.5 (68)		0 (41)	
22	Charlotte Harbor	7/18/93		1.3 (76)		0 (92)	
23	Sarasota Bay	7/19/93		2.2 (89)		0 (53)	
24	Tampa Bay	7/19/93		0 (91)	0 (19)	0 (63)	
25	Steinhatchee	7/20/93		2.7 (37)	4.3 (23)	0 (18)	
26	Panacea	6/15/93		3.7 (107)	3.1 (32)	0 (77)	
27	Apalachicola	6/15/93		4.3 (116)	3.6 (28)	2.1 (92)	
Total by host species =			2.4 (41)	2.3 (584)	3.6 (84)	0.5 (436)	23 (324)

species ($X^2 = 16.63$, $df = 2$, $P < 0.001$) and sites ($X^2 = 16.48$, $df = 5$, $P < 0.001$), and there were no significant interaction terms ($P > 0.5$). Rhizocephalan prevalence in *E. depressus* was notably variable among sites and between years (Site*Year: $X^2 = 11.02$, $df = 4$, $P < 0.05$), with high prevalences occurring at Quinby, Virginia in 1986 (83%) and in Bogue Sound, North Carolina in 1983 (47%), where prevalence dropped to 0% in 1986 (Bogue Sound, Year: $X^2 = 21.1$, $df = 1$, $P < 0.001$).

In 1993, supplemental samples from North Carolina and eight sites along approximately 750 km of the west coast of Florida included 1469 xanthid crabs composed of: 40% *Panopeus similis*; 30% *E. depressus*; 22% *Rhithropanopeus harrisi*; 6% *Panopeus obessus*; and 3% *P. lacustris* (Table 2). In these samples 94 crabs (6%) had parasite externaenae. Prevalence was relatively high (23%) in *R. harrisi* in the Neuse River, North Carolina and low (0-4.3%) in samples of *P. lacustris*, *P. simpsoni*, *P. obessus*, and *E. depressus* along western Florida. Considering only the 1993 samples along western Florida, log-linear models revealed significant variation among host species ($X^2 = 23.75$, $df = 3$, $P < 0.001$) but not among the eight sites ($X^2 = 5.53$, $df = 7$, $P > 0.5$) and no significant Host*Site interaction ($X^2 = 26.63$, $df = 21$, $P > 0.18$). Prevalence in *E. depressus* (mean = 0.5%, with parasite present at only one site) was significantly lower than in the three *Panopeus* species (mean = 2.5%, with parasite present at all but one site) ($X^2 = 6.56$, $df = 1$, $P = 0.01$). Prevalence differed significantly among the three *Panopeus* species ($X^2 = 15.98$, $df = 2$, $P < 0.001$) but not among sites for these hosts ($X^2 = 3.18$, $df = 7$, $P > 0.8$).

SPATIAL VARIATION WITHIN NATIVE AND INTRODUCED REGIONS. — Within the parasite's native range in the Indian River Lagoon, a total of 2296 xanthid crabs of three species was collected during June-August 1983 from six subsites: 59% *E. depressus*, 36% *P. lacustris*, and 5% *R. harrisi* (Table 3). Of these crabs, only 26 individuals (1.1%) exhibited *L. panopaei* externaenae. The prevalence of infection differed significantly among host species ($X^2 = 20.02$, $df = 2$, $P < 0.001$) but with a significant Host*Subsite interaction ($X^2 = 16.68$, $df = 8$, $P < 0.05$). The overall prevalence in *P. lacustris* was 3%, varying significantly from 0-9.3% among subsites ($X^2 = 9.32$, $df = 4$, $P > 0.05$). Only a single *E. depressus*

Table 3. Prevalence of *Loxothylacus panopaei* in xanthid crabs sampled within the Indian River Lagoon, Florida, in 1983. Map Loc. refers to Figure 1. Numbers indicate percent of sample bearing externaе (no. crabs in sample)

Map			<i>Panopeus</i>	<i>Eurypanopeus</i>	<i>Rhithropanopeus</i>
Loc.	Site	Date	<i>lacustris</i>	<i>depressus</i>	<i>harrisii</i>
A	Fort Pierce Inlet	8/10/83	0 (105)	0 (24)	
B	Little Jim Island	6/17/83	3.3 (153)	0.7 (144)	
		8/10/83	3.4 (327)	0 (244)	
C	Dredge Spoil Island I	8/8/83	1.8 (165)	0 (581)	
D	Dredge Spoil Island II	8/10/83	9.3 (54)	0 (78)	
E	Wabasso Causeway	8/9/83	4.3 (23)	0 (287)	
F	St. Lucie River	6/16/83			0 (111)
Total by host species =			3.0 (827)	0.1 (1358)	0 (111)
Total =			1.1 (2296)		

(0.1%) from five sites was infected, and no *R. harrisii* was infected at the single site of collection.

Within the parasite's introduced range in Chesapeake Bay, a total of 851 crabs of four xanthid species was collected during July-August 1983 from six sites: 43% *Panopeus herbstii*, 18% *E. depressus*, 29% *D. sayi*, and 9% *R. harrisii* (Table 4). Of these crabs, 19 individuals (2.4%) exhibited rhizocephalan externaе; and the prevalence differed significantly by host species ($X^2 = 14.95$, $df = 3$, $P < 0.002$) with a significant Host*Subsite interaction ($X^2 = 40.77$, $df = 15$, $P < 0.001$). The prevalence of infection for *E. depressus* averaged 9.6% but ranged from 2.2-90.9% with significant variation among subsites ($X^2 = 29.42$, $df = 3$, $P < 0.001$). Parasitism in *D. sayi* averaged 1.6% without significant variation among subsites ($X^2 = 4.45$, $df = 3$, $P > 0.2$). *P. herbstii* was not infected, nor was *R. harrisii* in this 1983 sample (but see below).

LONG-TERM TEMPORAL VARIATION AT ESTABLISHED AND INTRODUCED SITES. —The prevalence of rhizocephalan infection in *P. lacustris* at Jim Island near Fort Pierce in the Indian River Lagoon, Florida, was relatively constant (mean = 7.5%, range 0-13%) (Fig. 2) without significant differences among years over the 12-yr period from 1982-1993 ($X^2 = 18.23$, $df = 11$, $P > 0.1$).

The long-term pattern of prevalence of *L. panopaei* in *R. harrisii* at the Rhode River subestuary of Chesapeake Bay during the 15 yrs from 1979-1993 (Fig. 2) is in marked contrast to the stable pattern in *P. lacustris* in Florida. Prevalence differed significantly among years ($X^2 = 49.89$, $df = 14$, $P < 0.001$). After 7 yrs of sampling without detecting any parasitism at the Maryland site, parasitized *R. harrisii* appeared at low prevalence briefly in late summer-early fall 1986. The parasite re-occurred suddenly at higher levels (19%) in 1990, and by 1991 more than 70% of the population sample were parasitized. In 1993 prevalence declined sharply but remained at relatively high levels of 30-40%.

SIZE CHARACTERISTICS OF PARASITIZED HOSTS. —*Panopeus lacustris* parasitized by *L. panopaei* in the Indian River Lagoon, Florida, ranged in size from 7-20 mm carapace width and exhibited a distinct mode at 13 mm (Fig. 3), which was the size of onset of reproductive maturity for females. Ovigerous crabs attained a much larger maximum size of 42 mm and had a significantly larger mean size than parasitized crabs (Student's *t*-test, $t = 1.98$, $P < 0.001$). Mean size of parasitized crabs at 13.8 mm did not differ signifi-

Table 4. Prevalence of *Loxothylacus panopaei* in xanthid crabs sampled within Chesapeake Bay during 1983. Map loc. refers to Figure 1. Numbers indicate percent of sample bearing externae (no. of crabs in sample)

Map			<i>Panopeus</i>	<i>Eurypanopeus</i>	<i>Dispanopeus</i>	<i>Rhithropanopeus</i>
Loc.	Site	Date	<i>herbstii</i>	<i>depressus</i>	<i>sayi</i>	<i>harrisii</i>
G	Hampton, VA	7/11/83	0 (31)	9.1 (11)		
H	Gloucester Pt., VA	7/11/83	0 (28)	4.7 (43)	8.3 (12)	
I	Tangier Light, MD	8/10/83	0 (160)		0 (69)	
J	Janes Island, MD	8/16/83	0 (99)	2.2 (90)	1.1 (95)	
K	Great Rock, MD	8/13/83	0 (49)	90.9 (11)	2.7 (74)	
L	Rhode River, MD	8/1/83				0 (79)
Total by host species =			0 (367)	9.6 (155)	1.6 (250)	0 (79)
Total =			2.4 (851)			

cantly among years from 1982 to 1993 (repeated measures ANOVA, $F = 1.95$, $P > 0.05$) (Fig. 4).

Parasitized *E. depressus* were rare in the Indian River Lagoon but ranged in size from 7-13 mm carapace width with a mean of 11.1 mm (Fig. 3). This range spanned the smaller two-thirds of size of ovigerous female crabs, but this assessment is limited to only seven infected crabs. In Chesapeake Bay, parasitized *E. depressus* averaged 9.1 mm carapace width, ranging from 6-18 mm and including essentially all sizes of this species (Fig. 3).

Parasitized *R. harrisii* in the Rhode River subestuary in 1991 ranged from 5-14 mm, including essentially all sizes of this species (Fig. 3). Mean size of parasitized crabs at 7.8 mm did not differ significantly among years 1986, 1990-1993 (repeated measures ANOVA, $F = 0.89$, $P > 0.05$) (Fig. 4).

DISCUSSION

Loxothylacus panopaei exhibited a disjunct distribution over 14 degrees of latitude and 2750 km of shoreline along the east coast of North America (Fig. 1). The parasite's native range extends through the Caribbean, Gulf of Mexico (Boschma, 1955; Reinhard and Reischman, 1958), and up eastern Florida to a northern limit at about Cape Canaveral (Fig. 1). Following introduction from the Gulf of Mexico into lower Chesapeake Bay in the mid-1960s (Van Engel, 1966; Daugherty, 1969), this rhizocephalan has now spread through out most of the Chesapeake mesohaline zone, part way up the outer coast of the Delmarva Peninsula, and south into the sound system of North Carolina (probably via the Intracoastal Waterway) (Fig. 1). The parasite remained absent in our samples from South Carolina to northern Florida.

Some rhizocephalans may be host specialists (Boschma, 1955; Phillips and Cannon, 1978; Ritchie and Høeg, 1981; Herberts, 1982; Lützen, 1984; Hawkes et al., 1986; Johnson et al., 1986; Shields and Woods, 1993); while the host specificity of other rhizocephalans appears to be comparatively generalized. For examples, *Peltogaster paguri* infects four species of North Atlantic hermit crabs (Nielsen, 1970); *Briarosaccus callosus* parasitizes six lithodid species in the north Pacific (Boschma and Haynes, 1969); *Heterosaccus*

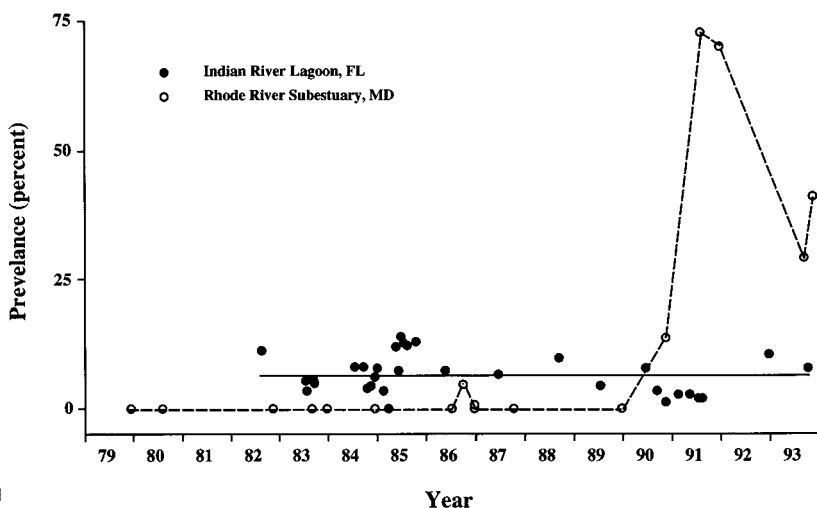


Figure 2. Long-term variation in prevalence of *Loxothylacus panopaei* in *Rhithropanopeus harrisi* from 1979-1993 in the Rhode River, Maryland and in *Panopeus lacustris* from 1982-1993 within the Indian River Lagoon, Florida.

californicus occurs in five brachyuran species along western North America (Boschma, 1955; O'Brien, 1984; personal observations); and *Sacculina carcini* parasitizes 12 species of European brachyuran crabs (Høeg and Lützen, 1985). The host specificity of *L. panopaei* appears to be relatively generalized, infecting at least nine species from the western Atlantic and Caribbean, including a goneplacid *Tetraplax quadridentata* and the xanthids *Tetraxanthus rathbunae* and *Panopeus occidentalis* (Boschma, 1955; Reinhard and Reischman, 1958), as well as six common species in our samples (*P. lacustris*, *P. simpsoni*, *P. obessus*, *E. depressus*, *D. sayi*, and *R. harrisi*). Due to limited morphological characteristics in these rhizocephalans, it may be argued that this apparent host generality may actually represent complexes of difficult-to-identify species which individually infect more limited host diversity. Future genetic analyses may reveal greater parasite diversity and concomitantly narrower host specificity. However, *L. panopaei* is capable of cross-infecting from *E. depressus* to *R. harrisi* in the laboratory (Alvarez, 1993). Moreover, infection of three host species by the introduced population of *L. panopaei* in Chesapeake Bay also suggests host generalization, especially since one species (*D. sayi*), reported here as a host for the first time, apparently was not parasitized in the initial stages of the introduction (Van Engel et al., 1966; Daugherty, 1969).

The parasite's prevalence varied within and among host species over the native and introduced range. *Eurypanopeus depressus* was parasitized both in native and in introduced regions, although prevalence in Florida was very low to nil. Within the parasite's native range in Florida, each of the three *Panopeus* species that we sampled was infected. In contrast, *L. panopaei* appears incapable of parasitizing *P. herbstii*. Although *L. panopaei* is reported to be common in *P. herbstii* from North America (Boschma, 1955), we found no infected specimens in our extensive samples over most of this host species' geographic range; and Daugherty (1969) did not find any infections in *P. herbstii* within Chesapeake Bay. This apparent discrepancy is probably an artifact of the hosts' recent taxonomic revision (Williams, 1983) partitioning the *P. herbstii* species complex into six species.

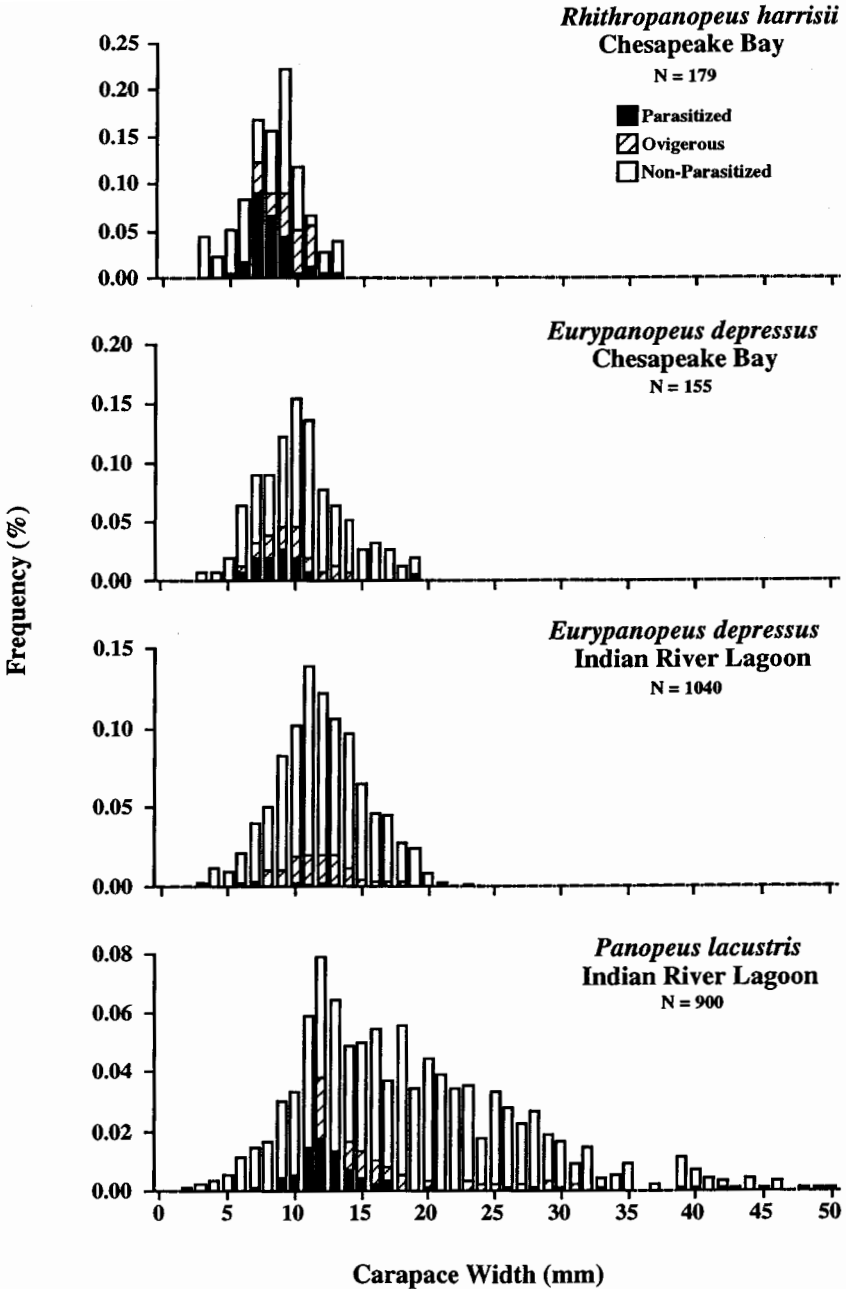


Figure 3. Size-frequency distributions of *Panopeus lacustris* and *Eurypanopeus depressus* in the Indian River Lagoon, Florida, and of *E. depressus* and *Rhithropanopeus harrisi* in Chesapeake Bay, Maryland. Histograms indicate non-parasitized crabs (open bars), parasitized crabs (solid bars), and ovigerous females (hatched bars). N = sample size.

Thus, the occurrence of *L. panopaei* in our samples of *P. lacustris*, *P. simpsoni* and *P. obessus* along the Gulf coast of Florida would have all been recorded as infections of *P. herbstii* prior to 1983. Interestingly, the revised southern limit of distribution of *P. herbstii* is Cape Canaveral, which coincides with the northern limit of the native range of the parasite. One host species (*D. sayi*) appears to be infected only within the introduced range of the parasite. Our data also suggest that *L. panopaei* only infected *R. harrisii* within the introduced region of the parasite. However, our collections sampled mainly high salinity habitats, where this crab species does not occur.

The size range of parasitized individuals reflects the demographics of host vulnerability (O'Brien and Van Wyk, 1984). Although the size range of crabs infected by *L. panopaei* was similar in three host species of our study, mature *P. lacustris* grew larger than parasitized crabs; whereas in *E. depressus* and *R. harrisii* the entire size-range of crabs appeared to be vulnerable. In *R. harrisii*, the stage which is infected may range from megalopa to older juvenile instars, resulting in a full size range of crabs with initial externa in this small host (Walker et al., 1992; Alvarez et al., 1995). In at least some rhizocephalan infections, the externa may drop off periodically, whereupon the host may molt and a new externa soon emerges, producing a range of sizes of infected hosts (Lützen, 1981; Alvarez, 1993; Takahashi and Matsuura, 1994). In these three crab species, we have occasionally observed individuals which have lost externae and retain scars on their abdomen. Clearly, however, *P. lacustris* has a size range of larger crabs which serves as a population refuge from infection, while *R. harrisii* and *E. depressus* do not.

Patterns of spatial variation in the prevalence of parasitism indicate that dispersal of this rhizocephalan operates on a scale of tens of kilometers. Within the Indian River Lagoon system, prevalences in our samples did not vary over distances of up to 20-30 km; while in the Chesapeake Bay infections varied over 100 km distances. On the scale of 1000 km, infections were highly variable and appeared quite "patchy" along the east coast of North America. The non-feeding planktonic larva of *L. panopaei* is short-lived at 25° C with a 2 d naupliar development to the cypris, which remains capable of infection for 2-4 d (Walker et al., 1992; Alvarez and Hines, unpub. obs.). This short planktonic phase would tend to limit dispersal away from the parental stock (Strathmann, 1974). The patchy pattern of infection in our samples is consistent with a distance of larval dispersal for a few days in typical current speeds of 0.25-0.5 km hr⁻¹ (Boicourt, 1982): 12-24 km over a 2 d larval life. Such short larval dispersal would not favor parasite transport to neighboring estuaries and embayments far along the coast if not bridged by suitable host populations; but it would favor rapid infection of local host populations.

Temporal variability in the prevalence of *L. panopaei* indicates three patterns of host-parasite dynamics: stable, sporadic, and epidemic infections. Rhizocephalan infections in *P. lacustris* within the Indian River Lagoon, Florida, were remarkably stable over a period of at least 12 yrs. In contrast, *E. depressus* in North Carolina exhibited highly sporadic parasite infections, with the prevalence fluctuating widely between years from a major infection of 47% initially to 0% 3 yrs later. A third epidemic pattern of *L. panopaei* occurred in *R. harrisii* in the Rhode River subestuary of Chesapeake Bay in the early 1990's after at least 7-10 yrs of no infection in this host population. This outbreak was probably part of the spread of rhizocephalans from their introduction into lower Chesapeake Bay in the early 1960's (Van Engel et al., 1966). By the late 1960's, rhizocephalans were common in *E. depressus* (10-70%) and *R. harrisii* (0-87%) throughout the lower Chesapeake Bay up to the Potomac River but had not spread to the upper bay, nor appar-

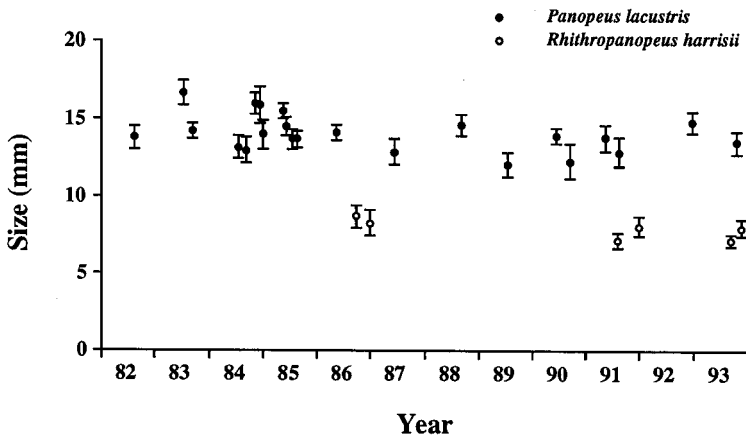


Figure 4. Temporal variation in carapace width of crabs parasitized by *Loxothylacus panopaei*: *Panopeus lacustris* (solid circles) in the Indian River Lagoon, Florida; and *Rhithropanopeus harrisi* (open circles) in the Rhode River subestuary of Chesapeake Bay, Maryland. Means and standard error bars are plotted.

ently out of the bay (Daugherty 1969). In 1983 our samples did not detect the parasite in the outer bays of the Delmarva Peninsula, although it apparently was found earlier in Chincoteague (Overstreet, 1978); but by 1986 high prevalences occurred up to Chincoteague but not beyond. Salinity limits the distribution of the parasite at about 10‰, providing a low salinity refuge for *R. harrisi* (Reisser and Forward, 1991). However, this apparently did not limit the parasite's distribution in the late 1960's, because extensive areas of the mesohaline zone remained uncolonized while the parasite extended to salinities of nearly 5‰ in lower bay tributaries (Daugherty, 1969). During prolonged periods of drought in the 1980's, salinities higher than 15‰ (well within the parasite's tolerance) frequently occurred in the Rhode River for periods of many months in several years (Jordan et al., 1991), and the parasite occurred briefly at this site in 1986. However, the 1990 outbreak of *L. panopaei* in the Rhode River did not coincide with any obvious shift in water quality variables or salinity (Jordan et al., 1991). Thus, this epidemic appears to reflect a lag of nearly 30 yrs for the parasite to disperse 200 km up the Chesapeake Bay from initial introduction, with the last 100 km from the mid-bay taking about 20 yrs. Spread to the North Carolina sound system may have occurred by the late 1970's or early 1980's (S.G. Morgan, pers. comm.). Like the spatial patterns, these temporal patterns of variation also indicate that *L. panopaei* has limited dispersal capabilities but can rapidly infect local populations.

Several aspects of the spatio-temporal variation in prevalence of *L. panopaei* in xanthid crabs may account for the parasite's persistence despite its impact on host reproduction. First, castrators interact with host species composition to stabilize both host and parasite populations, as shown for cryptoncid isopods in barnacles (Blower and Roughgarden, 1989). In our study, host species of varying susceptibility changed in relative abundance among sites along the geographic range of parasite distribution and along estuarine salinity gradients within many sites. Without long-term records of crab abundance, it is not clear whether the impact of *L. panopaei* on host populations can, in turn, produce shifts in

host species composition as postulated by Andrews (1980) for the lower Chesapeake Bay following the parasite's introduction. Second, Kuris and Lafferty (1992) suggest that population dynamics of crustacean fisheries infected by parasitic castrators should depend upon whether recruitment of the host and parasite populations is relatively "open" or "closed". The limited planktonic dispersal of the *L. panopaei* indicates relatively closed recruitment. Similarly, the crab larval behavior producing variable estuarine retention in these species (Cronin, 1982) indicates that host recruitment is also relatively closed. This host-parasite system may be useful for testing models for effects of recruitment dynamics in comparison to other, relatively open marine systems. Third, infections of other parasitic castrators are known to vary with host dispersion pattern and density (Blower and Roughgarden, 1989), such that the aggregation of xanthid crabs in patchily distributed oyster shell and rock rubble habitats would promote local infection while inhibiting pandemic infection (Grosholz and Ruiz, 1995). Fourth, Murdoch et al. (1987) proposed that stable parasitoid populations require the presence of an invulnerable host stage in combination with overlapping host generations and mixed aged classes to eliminate temporal gaps in the production of vulnerable host stages. All of the host crab species in our study produce multiple broods during warm months resulting in mixed age-classes when the parasite also is actively producing a rapid series of broods. Sporadic and epidemic infections of *L. panopaei* occurred in small crab species (*R. harrisii* and *E. depressus*), which lack a size class invulnerable to infection. By contrast, long-term host-parasite stability occurred in *P. lacustris*, which exhibits clear invulnerability at larger sizes. Variation in these attributes produces a mosaic of parasite prevalence along the east coast of North America.

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ADDRESSES: (A. H. H.) *Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037*; (F. A.) *Department of Zoology, University of Maryland, College Park, Maryland 20742*; PRESENT ADDRESS: *Colección de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, A.P. 70-153, C.P. 04510, D.F. México*; (S. A. R) *Smithsonian Marine Station at Link Port, 5612 Old Dixie Highway, Fort Pierce, Florida 34946*.